

In this same material from off Fiji at 40 to 50 fathoms, *Chrysalidinella dimorpha* (H. B. Brady) also occurs in the rather peculiar form shown here (Fig. 3 *a, b*). The sides are entire, the later chambers uniserial, and the terminal face with the apertures peculiarly arranged. There are probably several species of this genus which may be possible of separation.

Although all three of the species figured here occur together, they are distinguishable at a glance. The specimens of *Chrysalidinella* may be at once identified by the entire outline even before the uniserial chambers are noted. The two species of *Trimosina* are also strikingly different in general appearance. *T. simplex* has evenly placed and arranged chambers with small spinose projections extending backward at a decided angle, whereas *T. perforata* is a smaller but coarser form, the chambers relatively larger, the projections large and the whole test often twisted.

ZOOLOGY.—*The chromatropism of Mermis subnigrescens, a nemie parasite of grasshoppers.*¹ N. A. COBB, U. S. Department of Agriculture.

The adult female *Mermis subnigrescens*, when ripe for ovijection, has a way of moving her head in more or less horizontal curves;—her head, directed skyward, is waved in “circles,” now clockwise, now the reverse. This seemingly purposeful behavior occurs when she emerges from the soil and while she is ascending the herbage to deposit her eggs. Inasmuch as the head of the egg-laying female,—unlike that of the young female as well as that of the male (neither of which ever quits the subterranean darkness),—contains reddish transparent pigment rather definitely distributed with reference to certain cephalic nerves, the question arose whether we do not have here a phototrope² and an

¹ Received March 12, 1929.

² It is suggested that the mechanisms through whose activation the responses of organisms termed tropisms find expression be called “tropes;”—“tropism” to be taken in almost any of its more or less well accepted meanings.

These meanings (interpretations of various investigators,—see Mast, 1915) vary all the way from (1) “an inherent tendency to respond” (Standard Dictionary), to (2) an “irresistible” or “predictable” orientation as definite and mechanical as that of a magnetic needle; but whatever the accepted interpretation, the reaction-mechanism must always be present, and be a system of intimately connected elements or organs, as is the digestive system, for instance, or the excretory system. Since we have for this system of intimately connected elements no inclusive single descriptive term, and since it is found highly convenient, or even necessary, for purposes of thought and discussion mentally to “isolate,” and separately to denominate, the digestive system or enteron, and other systems, it is suggested that in behavior studies a like situation be met by a similar,

affirmative answer was forecast, for the obvious reason, among others, that, as the pigment must absorb certain light frequencies and transmit others, the absorption might well result in some such changes of energy as characterize vision. Very suggestive also is the fact that the transparent, colorless parts of the head immediately in front of, and alongside, the suspected phototrope condense light rays upon it. (See Fig. 1.)

Previous experiment showed the spectrum frequencies concerned in bringing about ovijection in this nema probably to be some of those in the light-blue and low violet region of the spectrum, together with red (also infra-?).³ It would therefore be natural to suspect, under all the circumstances, that the cephalic pigment characteristic of the adult female absorbs, and "makes use of," the frequencies *present* just previous to and during ovijection. Hence a wish, (1), to determine what frequencies are present during and just previous to natural ovijection; and, (2) to determine what frequencies are absorbed by the cephalic pigment.

In this field comparatively little seems to have been published, though somewhat pertinent papers by Crozier, Mast, and others exist. Investigators have been mainly occupied with the optics of the various colorless, transparent, organic elements; the relative location and probable function of certain pigments, usually dark or black (opaque); and the "migration" and other changes of pigment, such as visual purple, due to the action of light; and, of course, with the associated nervous and contractile elements. Little has been published with regard to tropism definitely due to the absorption of rays of a *particular* frequency solely by transparent, colored pigment (other than visual

but if possible better (to wit monosyllabic), terminology. The advantages of a monosyllable from which short, convenient adjectives, verbs, adverbs and other nouns can readily be derived, are almost too obvious to need mention,—tropic, tropically, to trope, troping, etc., etc. Most helpful, perhaps, will be its use as a component, e. g., in "chromatropé."

Primarily "trope" denotes action,—action that is in progress rather than completed. By metonymy the word denoting an action (here, what is called a reaction) may be applied to the (re)action-mechanism, i. e., in the present case, to the responding system of intimately connected organs.

Following this suggestion, we may speak of a reaction mechanism that aids or causes an organism to face toward or away from light, as a *phototrope*; a reaction mechanism used in orientation with reference to gravity, a *geotrope*, etc., etc., etc.; thus the statocystic mechanism of crustaceans is a species of *geotrope*.

Accordingly, certain cephalic apparatus of *Mermis subnigrescens* is here spoken of as a phototrope; or, better, because more specific, as a *chromatropé*,—inasmuch as its reactions apparently are to definite frequencies (colors) of the solar spectrum. *Glaucotrope* γλαυκος = blue) may prove to be even more precise.

³ *Species of Mermis*. Journ. Parasitology, 8: 66. 1926.

purple) located definitely with reference to nerves, these nerves themselves so located as possibly to be sensory.

SPECTROSCOPIC TEST OF THE PRESUMPTIVE CEPHALIC CHROMATROPE OF *Mermis subnigrescens*

One-third of a millimeter of the front end of an adult female *Mermis subnigrescens*, including the head, was ligated and cut off, and then mounted on a microscope slide in water. The head was examined under a 1.5 mm. apochromatic microscope objective, having a similar objective as a condenser, in such a way that the image would fill as much as possible of the microscope field with the color of the pigment. (See Fig. 1.) The microscope was fitted with a spectroscopic eyepiece.

Sunlight was taken from a planished aluminum reflector placed so that a maximum of sunlight was reflected through both instruments,—i.e., the above apochromatic-micro-spectroscope and a comparison spectroscope. The pigmented tissue was brought into focus, and then the iris diaphragm of the microscope thrown open, so as to admit a "flood" of light. This produced a spectrum fairly readily seen in a darkened room, notwithstanding the very high magnification.

Much of the violet end of the spectrum (well into

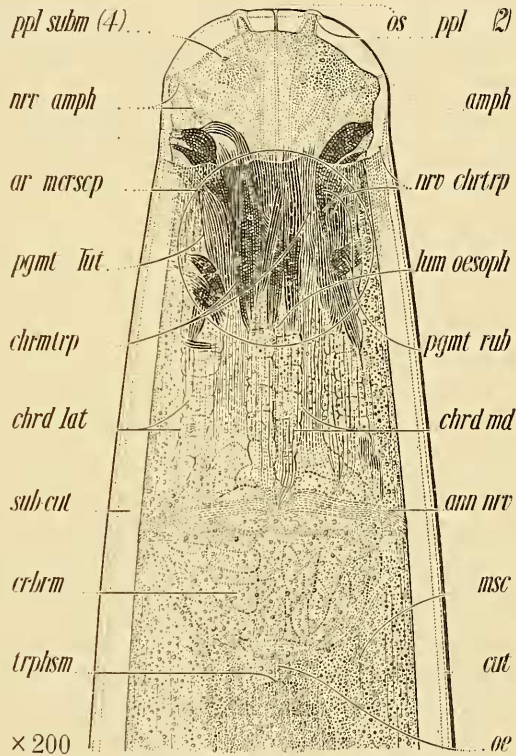


Figure 1. Head end of *Mermis subnigrescens*, showing the chromatrope. *os*, mouth; *ppl* (2), the two lateral so-called "papillae;" *amph*, amphid; *nrv chrtrp*, nerves of the chromatrope; *lum oesoph*, lumen of the oesophagus; *pgmt rub*, reddish pigment of the chromatrope; *chrd md*, median chord; *ann nrv*, nerve-ring; *msc*, body-wall muscles; *cut*, cuticle; *oe*, oesophagus; *ppl subm* (4), the four submedian papillae; *nrv amph*, nerve of the amphid; *ar merscp*, shows the circular area of the microscopic field that was tested spectroscopically; *pgmt lut*, orange-colored pigment of the chromatrope; *chrmtrp*, chromatrope; *chrd lat*, lateral chord; *sub cut*, the thick subcuticle; *crbrm*, the cerebrum; *trphsm*, anterior end of the trophosome.

the blue) was absorbed to a very considerable degree by the living cephalic pigment of the *Mermis subnigrescens*. The microscope field was never completely and uniformly filled with the color of the pigment. There were streaks at each margin of the field, and another through the middle, that showed little color (see Fig. 1), so that doubtless the absorption was not so pronounced as would be obtained by dissolved pigment of equal density filling the entire field of the microscope.

A satisfactory demonstration was made by placing the object under the microscope so as to produce absorption, and after the spectra had been arranged for comparison, suddenly removing the pigmented tissue. *The effect produced by this instantaneous change was very pronounced.* The blue and violet region of the spectrum, hitherto obscured by absorption, of course instantly assumed the same colors as in the comparison spectrum.

There seemed also to be some absorption in the outermost part of the red of the visible spectrum, but, if so, it was very slight. No absorption was noticed in the orange, yellow and green, and little if any in the bluish green.

The experiment was particularly satisfactory in that the pigment was *in a living condition*. True, the head had been ligated and cut off immediately before the spectroscopic examination, but from much experience it is known that such a head continues to live and move anywhere from a few hours to a day, or even more.

Phototropes of somewhat the character here described probably occur in the cervical region of many other nemas, particularly free-living ones,—the outer tissues of the neck serving as a cylindrical lens for condensing light upon the pigmented tissues. Aquatic nemas so situated as to utilize light rays penetrating water, not infrequently present structures that may be suspected to be phototropes,—now that we have a clue to the nature of such structures in this phylum. These primitive phototropes may well have been the forerunners of the more highly developed phototropes, ocellate systems, of certain nemas (e.g. *Enchelidium*).

A general review of the nature and relationships of localized transparent pigments in organisms in the light of the foregoing experiment, may, perhaps, suggest new ideas and experiments with regard to their functions both in animals and plants.

NATURAL CONDITIONS UNDER WHICH *Mermis subnigrescens*
DEPOSITS ITS EGGS

At Woods Hole, Mass., U. S. A., on July 28, 1928, from long before daylight up to 10 o'clock A.M. the weather was warm and showery. The showers were gentle but subcontinuous, with light-intervals between; *i.e.*, during two or three brief intervals the sunlight actually came through the fog and clouds rather clearly.

Two full-grown female specimens of *M. subnigrescens*, very much alike, were found depositing eggs naturally on grass etc. in an experiment field. As each nema still contained a good many eggs, both were taken to the laboratory in cold tap-water, and both subjected to radiant heat of low frequency, emanating from hot steel. The results of three trials on one of the nemas and four on the other were quite consistent.

An ordinary steel file about nine inches long and three-fourths of an inch wide was heated until hot, though not red. As near as could be judged the temperature of the file during the trials was from 400°–500° C. The hot steel was held within an inch and a half to two inches of the nemas. Held at this distance from one's cheek, it caused an agreeable warm sensation;—no disagreeable sensation of heat, however,—no suggestion of scorching.

When the nemas were brought into the laboratory, both were still slowly depositing eggs; one, however, very slowly,—putting out only one or two eggs semi-occasionally. When one of these ten-centimeter nemas in this laboring condition was removed from water and stretched out on a broad-leaf plantain, *Plantago major*, and the hot file brought near, she immediately responded by increased rapidity of movement, and in from ten to twenty seconds became coiled, sometimes rather closely, so that the entire space occupied by her would not be over fifteen to twenty millimeters across. Barely enough water was used on the plantain leaf so that only at her points of contact with the leaf was she in contact also with water. Doubtless the warmth may have caused the water to evaporate a trifle more rapidly, notwithstanding the saturated condition of the atmosphere, and one cannot say that this change in rate of evaporation may not have had some effect on the behavior, but the inevitable inference is that the "radiant heat" caused the change in behavior, corroborating, in a reverse way, experiments of previous years with direct sunlight and sunlight passed through heat-diminishing screens (both green glass and living foliage).

After the nemas had been rayed and returned to water in a watch-glass, and after they had resumed their former less active somewhat outstretched state, they were tested again and again with the infra-red rays. Two observers, noting the nemas before they were removed from the watchglass of water and after they had been rayed, declared the ovijection to be stimulated, and in one case the stimulation to be very marked indeed. In this case, at the time when the nema was removed from the glass, oviposition was diminishing to almost nil, only now and then an egg being deposited,—at intervals of half a minute or thereabouts; however, after she had been rayed and returned to the water where her behavior could be observed more accurately, deposition was going on vigorously,—batches of something like twenty eggs were being ejected at intervals of five to ten seconds. It should be remembered that these two females *already had their egg-laying capacity partially exhausted* and were therefore probably less favorable specimens for experiment than if they had just issued from the ground.

The conclusions drawn from the experiments were that, without doubt, *the radiant heat from the hot steel met with instant response by the nema and that the response was very definite and that the egg deposition was very markedly stimulated by the rays.*⁴

Apart from ultra-violet, apparently very little is known about the relative *amounts* of various light frequencies that are passed through different quantities of fog and watery vapor in the atmosphere. It is known that fog and vapor are more or less impervious to ultra-violet, but pervious to many other frequencies, among them blue and a certain amount of red and infra-red. However, nobody appears to have devised a method or instrument by which the amount of any particular one of these various other frequencies penetrating *under various atmospheric conditions* can be satisfactorily measured, although there is reason to hope that such data can be established.

It is very evident, however, that during the morning under consideration, which was showery with light rain much of the time, the weather varying all the way from thick fog to almost sunny,—fog so thick that the fog-horns were blowing, and yet at times the sky toward the east such that the sunlight came through rather clearly,—it is very evident that the amount of any given spectrum frequency reaching the experiment field probably would vary during the morning nearly through the entire daylight scale, or at least much of it.

⁴ But whatever stimulus, if any, the nema received from the sky was not sufficient by itself to cause any marked oviposition.

APPLICATION TO THE OVIJECTION OF *Mermis subnigrescens*.

The observations to date seem to shut out the possibility that ultraviolet has much of anything to do with ovijection taking place naturally in the open. The present observations seem *again* to make it exceedingly probable that radiant heat must have much to do with it. Recalling that the early morning light is relatively rich in red and infra-red, and that as moisture (dew, rain) is essential, or at any rate highly favorable, to the oviposition of *M. subnigrescens*, then obviously early morning and forenoon would be a favorable time of day for the oviposition. It is certain, from spectroscopic tests made during the morning in question, that *all* the time after sunrise a good deal of blue light was being passed through the atmosphere; and it therefore might have been a behavior stimulus, and no doubt was so.

All this harmonizes with previous experiments on the ovijection of this species,—an account of which is already published,—and explains the motive for the tests described above.

Thus we have a fairly complete theory of the above-ground egg-laying activities of *Mermis subnigrescens*. When the nema is ripe for labor, she moves from her pitch dark, subterranean "domicile" to the surface of the ground. Her movements during this trip no doubt exemplify apogeo-, hydro-, thermo-, rheo-, thigmo-, and finally, just before she reaches the surface, photo-tropism.

Once her head is free of the surface of the ground, her chromatrope comes into full play, "detecting" the direction and amount of light from the sky, particularly, perhaps only, blue light. The structure of the chromatrope is particularly adapted to the reception of light *from above* or *from any side*, for the light will be concentrated in the chromatrope by the transparent front tissues of the head acting as a hemispherical lens, and the side tissues acting as a cylindrical lens.

As she clambers higher and higher on the herbage, she responds to such blue sky light as is not intercepted by the green blades of grass and other foliage above and around her. Led by the blue light and the urge to deposit, she will at last reach an elevation on the herbage subject to a more direct action of the sun's rays, when the ovijector and uterine muscles will be affected by red rays and ovijection will begin; and this place in many instances would be *at the altitude of grazing grasshoppers*, the definitive hosts.

This would be a new and special parallel to the ordinary sequence of events in ovijection and parturition. In other words the "voluntary" nervous system comes first into play, bringing the organism into con-

ditions favorable to the events about to follow. Thereafter the behavior is more or less "involuntary," as has been shown in the present instance by the fact that ovijection continues under the stimulus of sunlight, even if the head, including the chromatrope and central nervous system, be removed,—seared off.

CIRCUMSTANTIAL EVIDENCE FOR THE CHROMATROPISM OF
Mermis subnigrescens

1. The commonly infested grasshoppers graze mostly within certain limits above the ground; harmoniously, the eggs of the mermithid parasite are found to occur preponderantly within these limits, suggesting highly developed egg-laying instincts on the part of the nema that might well presuppose tropism.

2. A definite mechanism, believably a phototrope [includes chromatrope, (includes glaucotrope)] embodying what are believably receptors, transmitters, and effectors, is present;—a mechanism not otherwise readily explicable. The only mermithid individuals known to possess such a mechanism fully developed are those whose *blackish eggs are deposited in the way* characteristic of *Mermis subnigrescens*.

3. The putatively-chromatropic pigment absorbs,—i.e., can be sensitive to,—blue rays.

4. Only adult, chromatroped, egg-laying females clamber as described. Males and young females having no power, or occasion, to deposit eggs are not chromatroped.

5. The clambering of the nemas ripe for oviposition is skyward;—*i.e., toward blue sky, rather than vertical* (distinction from negative geotropism). Beams of blue light *from the sky*, often oblique, and coming from many widely different directions, are those most certain promiscuously to penetrate the depths of the herbage, and thus reach to near the ground. The nema's lens-like tissues concentrating light upon the chromatrope, accept it from above and from all sides; this harmonizes with the distribution of blue sky light.

6. Oviposition is stopped, or very much slowed, by green screens (including living foliage) that absorb red and infra-red; indicating a necessity for the nema to escape from exclusively green light before oviposition can take place. In the grasshopper habitats, blue light (sky-light) is the most diffused and most likely to be useful in leading to the known consummation, should chromatropism come into play at all. In nature, clambering skyward ("blue-ward") from out the green, brings the nema soonest under the incidence of the longer wave lengths so stimulative to the ovijectors.